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Ecophysiological, Ecological, and Soil Processes in Terrestrial Ecosystems: A Primer on General Concepts and Relationships

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A.1. Introduction

All living organisms in terrestrial ecosystems ultimately depend directly or indirectly upon photosynthesis for their energy requirements. Photosynthesis depends on the absorption of light and the diffusion of CO_2 from the atmosphere to the sites of photosynthesis within leaves. To take up CO_2, plants must open their stomata; this generally results in considerable water loss. Increases in atmospheric CO_2 concentration can reduce water loss and increase photosynthetic carbon gain of most plants. Plant growth is only possible if temperatures are between some lower and upper thresholds; plant growth at most locations is likely to increase with moderate increases in annual mean temperature, mainly due to lengthening of the growing season.

Plants also need inorganic nutrients from the soil, such as nitrate or ammonia and phosphate, and plant response to environmental variables is modified by the availability of these soil nutrients. Furthermore, soil-nutrient availability itself can also be affected by environmental factors.

At any site, there are usually many different plant species that interact with each other and with other organisms in a multitude of different ways. In considering the effect of climate change on any terrestrial ecosystem, it is necessary to consider not only the direct ecophysiological effects in response to climate change but also the ways in which these direct effects are modified by soil feedbacks and biological interactions between different organisms.

Because many of the responses of terrestrial plants in diverse ecosystems are similar, a general description is offered here of some of the major potential impacts of climate change on terrestrial ecosystems (see also Chapter 9, *Terrestrial Biotic Responses to Environmental Change and Feedbacks to Climate*, of the IPCC Working Group I volume). This primer initially provides some overview of effects of the most important climatic driving forces that are likely to change, then discusses effects on soil carbon and nitrogen dynamics, looks at soil fertility as a modifying effect on responses to external driving forces, and includes a brief discussion of soil biological factors. These broad ecosystem responses are modified by ecological interactions between the different organisms in each ecosystem; the primer provides a brief overview of the major ecological factors that must be considered in assessing the impact of climate change on terrestrial ecosystems.

A.2. Climatic Driving Forces

Solar radiation, temperature, precipitation, air humidity, and atmospheric CO_2 concentration are some of the most important external forces that drive ecosystem processes. Precipitation, air humidity, and other meteorological variables—as well as plant and soil variables—together determine water availability for plants. Of these, changes in temperature, water availability, and CO_2 concentration are likely to constitute the most significant changes for terrestrial ecosystems over the coming century. The effects of these changes are discussed in the following sections.

A.2.1. Temperature

The increase in CO_2 and other greenhouse gases is expected to cause an increase in global mean temperature, with larger increases at high latitudes than elsewhere and larger increases during winter than summer (Gates *et al*., 1992; Greco *et al*., 1994). Plant growth and health may benefit from increased temperatures because of reduced freezing and chilling damage, but plants may be harmed by increased high-temperature damage. There is some indication that higher mean temperatures in the future will be associated with more variable and more extreme temperatures (Katz and Brown, 1992). However, the increase in global mean temperature during the past half-century has been primarily a result of higher night temperature (Karl *et al*., 1993).

Net primary productivity (NPP) is generally enhanced by modest increases in temperature, especially in temperate and boreal regions (e.g., Kauppi and Posch, 1985; Cannell *et al*., 1989; Kokorin *et al*., 1993; Beuker, 1994). According to a relationship developed by Lieth (1973) based on observed net primary production in a variety of ecosystems, NPP will increase from 1% per °C increase in temperature in ecosystems with a mean annual temperature of 30°C to 10% per °C at 0°C. However, because this relationship is based on observations of NPP under present temperatures, part of the apparent increase could be the result of a correlation between higher solar radiation and higher temperature, so the actual effects of temperature change alone may be smaller.

Effects of increasing temperature on crop yields are more difficult to predict than effects of temperature on NPP because crop yields are not only affected by NPP but also by the phenology of crop development (see also Chapter 13). Increased temperature can speed phenological development, reducing the grain-filling period for crops and lowering yield—as is observed in current conditions (e.g., Monteith, 1981) and in most modeling studies (Warrick *et al*., 1986; Chapter 13). For example, Wang *et al*. (1992) modeled the growth of wheat with climate change, and found that yield decreased as temperature increased because crop development was hastened. A cultivar from a warmer region, however, responded positively to moderate increases in temperature and gave a larger yield than the cultivar from the colder region under current conditions. This suggests that current cultivars might generally perform more poorly in a warmer climate, but losses could generally be avoided by cultivar substitution.

Extreme temperatures are often more important than average temperatures in determining plant responses (Woodward, 1987). If global warming reduces the frequency of extremely low temperatures, plants may be able to survive at higher latitudes or altitudes, and agricultural plants can be grown for longer periods of the year without the danger of damaging frosts. On the other hand, many plants are adapted to the climate in their current locations, and a general warming could result in premature bud-burst and so, paradoxically, increase frost damage (Hänninen, 1991). Alternatively, plants may experience insufficient chilling exposure so that flowering and

fruit and seed production may not proceed at all, or be initiated in a season with inappropriate climate. In another study, increased temperature was found to speed bud-burst, but increasing CO_2 concentrations counteracted the effect, in some locations completely (Murray *et al*., 1994).

Increased episodes of extremely high temperature can damage plants, especially in conjunction with water shortage. However, if sufficient soil water is available, leaf temperatures can be substantially lower than air temperature as a result of evaporative cooling. Burke *et al*. (1988) report that many plants maintain leaf temperatures within a preferred range, thereby optimizing NPP. While the amount of water consumed for leaf cooling can be substantial and highly variable, typically 200–500 water molecules may be lost for each molecule of CO_2 taken up (Sharkey, 1985). This can lead to insufficient water in plant tissues, resulting in reduced growth. Elevated CO_2 reduces stomatal conductance (Eamus, 1991) and so saves water, but this may further increase the temperature of leaves, over and above increased air temperature.

Plant membranes may be damaged at high temperature (Berry and Björkman, 1980), and membranes in plants are often modified following growth in high temperature. However, this reduces plant performance at low temperature. High temperature can affect other plant processes. Respiration rates are often increased by high temperatures, and plant respiration can account for the loss of a significant fraction of the carbon fixed in photosynthesis. However, plants may acclimate to higher temperature, and the short-term effects of temperature on respiration are often not seen when plants are grown at different temperatures (e.g., Gifford, 1994; Körner, 1995). Also, the response of leaf respiration rate to temperature can be substantially reduced in plants grown in high CO_2 and high temperature (e.g., Wullschleger and Norby, 1992). The interaction between increased temperature and increased CO_2 is substantial, and the effect of warming by itself may be modified or even reversed when CO_2 effects are considered. Other processes—such as the volatilization of hydrocarbons, which could affect carbon balance—show less acclimation to high temperature (Tingey *et al*., 1991; Lerdau 1991). Hydrocarbon loss from leaves can exceed 10% of the carbon taken up for photosynthesis.

A.2.2.   *Precipitation and Soil Water Availability*

Active physiological processes of plants require an aqueous medium. Higher land plants are able to survive within a generally dry atmosphere because they are covered by a cuticular epidermis that minimizes water loss. For growth, however, plant leaves must take up CO_2 from the atmosphere. This need for a path for diffusion of CO_2 into the leaves also provides a path by which water is lost from leaves. Water loss is regulated by stomata whose aperture is adjusted in response to environmental variables and internal regulators.

If the soil is wet, plants can replace transpired water with water from the soil. If plants continue to extract water from the soil,

and if soil water is not replenished by rain or irrigation, then the water content of plants must eventually fall and their physiological function is impaired (Hsiao, 1973; Bradford and Hsiao, 1982). Water-stressed plants restrict further water losses by closing stomata, by adjusting the angle at which leaves are held to minimize light absorption, or by shedding leaves (Passioura, 1982). CO_2 uptake and growth is then reduced or completely prevented (Schulze and Hall, 1982). Water availability at most locations is seasonally variable, with plants experiencing at least temporary drought for some time (Woodward, 1987; Stevenson, 1990). Individual species are adapted to particular water regimes and may perform poorly and possibly die in conditions to which they are poorly adapted (e.g., Hinckley *et al*., 1981).

Total plant growth under water-limited conditions is essentially given by the product of the amount of water used and water-use efficiency. Short-term water-use efficiency can be expressed as the ratio of the difference of CO_2 concentration between the atmosphere and the sites of photosynthesis to the difference of water-vapor concentration between the sites of evaporation within leaves and the atmosphere. Hence, anything that changes either of these concentration differences can potentially affect water-use efficiency and thus growth under water-limited conditions (Eamus, 1991).

Different plant types (see Box A-1) have different water-use efficiencies. C_3 plants have relatively poor water use efficiency. C_4 plants have higher water-use efficiency because they photosynthesize at lower internal CO_2 concentration and thereby increase the difference in CO_2 concentrations between the atmosphere and the sites of photosynthesis. In CAM plants, CO_2 uptake occurs at night, when leaves are coolest and the leaf to air water vapor concentration difference is smallest. This gives CAM plants the highest water-use efficiency of all plants.

Higher CO_2 concentration generally leads to lower stomatal conductance (Kimball and Idso, 1983; Morison, 1987) and higher leaf photosynthetic rates (Eamus and Jarvis, 1989; Arp, 1991). This improves water-use efficiency, so carbon gain for plants with limited water supply should increase with increasing CO_2 concentration (Rogers *et al*., 1983; Idso and Brazel, 1984; Tolley and Strain, 1985; Morison, 1987; Eamus and Jarvis, 1989).

Many ecosystems experience shortage of soil water (drought) during some or most of the year, which limits their potential carbon gain (Lieth, 1973; Hinckley *et al*., 1981; Woodward, 1987). Soil water availability can be related to the ratio of precipitation to potential evapotranspiration, or to other measures of water availability, such as the ratio of actual to potential evapotranspiration. What is important in all these measures is that soil water availability can be affected by changes in either gains (precipitation) or losses (evapotranspiration) of water.

Because warmer air can hold more water, it is likely that increasing temperature will lead to a larger difference between the water-vapor concentration inside leaves and in the air, with

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Box A-1. Different Plant Groups

C_3— C_3 is the most basic photosynthetic mechanism. It is called C_3 because the first compound into which CO_2 is incorporated is a compound with three carbon atoms. C_3 plants make up the majority of species globally, especially in cooler or wetter habitats; they include all important tree and most crop species, such as wheat, rice, barley, cassava, and potato.

C_4— C_4 plants have a special CO_2-concentrating mechanism within their leaves by which they can increase the CO_2 concentration to several times above ambient levels. This is done by CO_2 first being incorporated into a 4-carbon compound. This allows these plants to maintain lower intercellular CO_2 concentrations than C_3 plants. C_4 plants tend to grow in warmer, more water-limited regions, and include many tropical grasses and the agriculturally important species maize, sugarcane, and sorghum.

CAM—Crassulacean acid metabolism, CAM, is a variant of C_4 photosynthesis in which CO_2 is not only concentrated but also stored for half a day. CAM plants, such as cacti, often grow in deserts, but they also include more common plants such as pineapple. In these plants, CO_2 uptake occurs at night. The CO_2 is then stored for use in normal photosynthetic reactions during the next day.

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little effect on the difference in CO_2 concentrations—thus lowering water-use efficiency. If the absolute humidity increases in line with the saturated humidity at the diurnal minimum temperature, and if both diurnal minimum and maximum temperatures change similarly with global warming, then the leaf-to-air water-vapor concentration differences will increase by about 5–6% per °C warming. However, if nighttime temperatures were to increase more than daytime temperatures—as has been the case over recent decades (Karl *et al*., 1993)—then the concentration difference will increase by less than 5–6% per °C.

General circulation models (GCMs) suggest that there are likely to be regions where precipitation will increase by more than the global average and where the additional rainfall may be more than sufficient to meet increased evaporative demand, whereas other regions may receive less rainfall than at present (Mitchell *et al*., 1990; Greco *et al*., 1994); this is further complicated by feedbacks from the biosphere. Henderson-Sellers *et al*. (1995), for example, show that inclusion of stomatal closure in response to increasing CO_2 concentration led to a reduction in the predicted increase in precipitation from 7.7% for doubled CO_2 to only 5.0%. The timing of water availability within ecosystems may also change. For example, earlier melting of snowpacks may mean that less water is available during summer (Mitchell *et al*., 1990; Hayes, 1991). There will therefore almost certainly be some regions with improved and others with worse water balances than at present.

Potential evapotranspiration rates can be estimated using a variety of meteorological formulae with varying physical rationales. Some workers have used the Thornthwaite method, which is based on correlations between evapotranspiration and temperature in the current climate (e.g., Thornthwaite, 1948; Le Houerou *et al*., 1993). Based on the Thornthwaite method, these workers conclude that water may become more limiting with temperature increase in the future (e.g., Gleick, 1987; Rind *et al*., 1990; Leichenko, 1993). However, the formulae that have the soundest physical bases—the Penman, Priestley and Taylor, and Penman-Monteith equations (Jarvis and McNaughton, 1986; Martin *et al*., 1989)—predict that potential evapotranspiration would increase with warming by an amount similar to the anticipated increase in precipitation (McKenney and Rosenberg, 1993), provided other factors such as radiation balance and surface resistance do not change. There would then be little change in the global incidence of drought conditions.

Where climate change leads to annual or seasonal changes in water availability, agricultural and forest productivity could change. Significant reductions in soil water availability could lead to forest decline. There could also be indirect problems, such as more floods and greater erosion hazards caused by more intense rainfall. Wind erosion could increase if drought lengthens the time that the ground is bare of vegetation. Changes in the ratio of precipitation to potential evapotranspiration could also affect water discharge into rivers and groundwater reservoirs.

If water runs off the surface instead of infiltrating the soil, the amount available to plants is reduced; this may also lead to erosion. Water infiltration rates are affected by soil texture and structure, slope, vegetation cover, soil surface roughness, surface crusting, and land management. Infiltration is also controlled by soil water content because saturated soils are unable to absorb water and very dry soils can be slow to re-wet. Aggregated soils with good structure facilitate infiltration, and aggregation is strongly affected by the organic matter content of the topsoil. Surface runoff is also strongly dependent on the amount and intensity of rainfall, which in most regions is likely to increase with climate change (e.g., Gordon *et al*., 1992).

The water-retention capacity of different soil types can influence the intensity of water stress experienced by plants. Soil water retention is significantly affected by soil organic-matter content, particle-size distribution, bulk density, and soil structure. Thus, any decrease in the quantity of soil organic matter as a result of faster decomposition could reduce infiltration rates and soil water retention and accentuate plant water stress.

Waterlogging can develop because of rising groundwater tables or because of the presence of partially permeable layers within the soil profile. Waterlogging can affect plant growth in both agricultural and natural environments by limiting the diffusion of oxygen to plant roots and soil organisms. Excess soil wetness can also be a considerable hindrance in agriculture by impeding soil tillage (Rounsevell and Jones, 1993), and climate change can thus affect crop production by affecting soil workability (Rounsevell et al., 1994).

A.2.3.   *Direct Effects of CO_2 Concentration*

Atmospheric CO_2 is a basic substrate for photosynthesis, which underlies plant growth. In the response of plants to CO_2 concentration, it is important to distinguish between plants with the C_3 and C_4 photosynthetic pathways. Increasing CO_2 concentration directly affects photosynthesis in three ways. Firstly, the carboxylating enzyme for carbon reduction in all plants, Rubisco, has a poor affinity for CO_2. The present atmosphere results in CO_2 concentrations in chloroplasts that are well below half-saturation (Farquhar and von Caemmerer, 1982). Consequently, the photosynthetic rate is very responsive to small increases in CO_2 concentration in C_3 plants. Secondly, oxygen competes with CO_2 for the active site on Rubisco, leading to photorespiration (Farquhar and von Caemmerer, 1982). The rise in atmospheric CO_2 concentration will progressively reduce photorespiration and enhance quantum yield of carbon fixation in C_3 plants. This will not occur in C_4 plants, which have a CO_2-concentrating mechanism that already suppresses photorespiration. Thirdly, stomata in many species progressively close as the atmospheric CO_2 concentration increases, thus reducing water loss relative to carbon gain. This gain may be offset to some extent by increased leaf temperature. It has also been argued that CO_2 will alter respiratory activity. Experimental evidence demonstrates both increases and decreases in response to increasing atmospheric CO_2 concentration (e.g., Amthor, 1991; Poorter et al., 1992).

It is well-established that short-term photosynthetic rates in C_3 plants increase by 25–75% for a doubling of CO_2 concentration (Kimball, 1983; Cure and Acock, 1986; Eamus and Jarvis, 1989; Allen, 1990; Bazzaz, 1990; Bowes, 1993; Luxmoore et al., 1993). There are fewer data available for C_4 plants. While some workers have found little response (e.g., Morison and Gifford, 1983; Henderson et al., 1992), others have found increases of 10–25% in photosynthetic rate for a doubling of CO_2 concentration (e.g., Wong, 1979; Pearcy et al., 1982; Polley et al., 1992). The sensitivity of C_3 photosynthesis to CO_2 concentration increases with increasing temperature (Long, 1991; Bowes, 1993; Kirschbaum, 1994); hence, the stimulation of plant growth by increasing CO_2 concentration is likely to be larger at higher temperatures (Idso et al., 1987; Rawson, 1992), with little stimulation and sometimes even inhibition at low temperatures (Kimball, 1983).

The increased photosynthetic rate and decreased water require-

ment translate into increased growth and crop yield of C_3 plants (Kimball, 1983; Cure and Acock, 1986), increased growth of C_4 plants (Poorter, 1993), and increased tree seedling growth (Luxmoore et al., 1993). However, this connection can be confounded by many factors. Firstly, acclimation of photosynthesis may occur such that photosynthetic capacity is diminished. An average 21% decrease in photosynthetic capacity has been observed in tree species (Gunderson and Wullschleger, 1994), although this may be an artifact of pot size (Arp, 1991; Thomas and Strain, 1991; Sage, 1994). Despite this decline in capacity, photosynthetic rate per unit leaf area was on average 44% higher in elevated than in ambient CO_2 (Gunderson and Wullschleger, 1994). Where reductions in photosynthetic capacity cannot be due to restricted rooting volumes, they are most likely a consequence of nitrogen shortage and reduction in Rubisco activity (e.g., Ceulemans and Mousseau, 1994).

Secondly, it is generally observed that carbon partitioning is altered, resulting in plants in elevated CO_2 having lower leaf area per unit of plant dry weight (e.g., Poorter, 1993), and the proportional increase in aboveground growth is less than the increase in photosynthesis or total growth. Responses may also differ in conjunction with other environmental limitations and between species (Gifford, 1992; Luxmoore et al., 1993).

Because the atmospheric CO_2 concentration has already increased from a preindustrial concentration of about 280 ppmv to about 360 ppmv at present, there should be evidence of increased growth of plants under natural conditions. However, the evidence from tree-ring chronologies is unclear (Innes, 1991). For example, Graumlich (1991) found no growth enhancements at five subalpine sites in the Sierra Nevada (California), but LaMarche et al. (1984), Kienast and Luxmoore (1988), Hari and Arovaara (1988), Cook et al. (1991), West et al. (1993), and Graybill and Idso (1993) observed varying degrees of growth enhancement in recent times compared with preindustrial times. However, part or all of that increase can probably be explained by more favorable temperatures and nitrogen fertilization by moderate levels of industrial pollution, especially as some of the observed increases are far greater than would be expected from CO_2 enrichment alone (Luxmoore et al., 1993).

There is increasing experimental evidence available on the effects of CO_2 enrichment on ecosystem dynamics, although much is still unpublished. The few results available to date give a divergent picture (Körner, 1995). For example, in a warm and nutrient-rich temperate wetland in Maryland, a high and persistent increase in growth has been observed (Curtis et al., 1989; Drake, 1992). Körner and Arnone (1992) observed an 11% increase in biomass over 100 days in an artificial tropical ecosystem; shoot biomass increased by 41% in a California grassland (Jackson et al., 1994), and midseason CO_2 uptake increased substantially in a Swiss alpine grassland (Diemer, 1994). On the other hand, almost no response to CO_2 enrichment has been observed in a cold and nutrient-limited tundra environment (e.g., Tissue and Oechel, 1987). In summarizing

ecosystem experiments, Körner (1995) found generally enhanced net CO_2 assimilation but little or no increase in aboveground biomass or leaf area and a likely increase in soil carbon.

Because water-use efficiency can be greatly enhanced by increased CO_2 concentration (Rogers *et al*., 1983; Tolley and Strain, 1985; Morison, 1987; Eamus and Jarvis, 1989), relative plant responses to increases in CO_2 should be most pronounced under water-limited conditions (e.g., Gifford, 1979; Allen, 1990). This difference between well-watered and water-limited conditions should be most pronounced for C_4 plants (Samarakoon and Gifford, 1995). Growth enhancement by CO_2 is also evident under severe nutrient limitation (e.g., Wong, 1979; Norby *et al*., 1986; Idso and Idso, 1994; Lutze and Gifford, 1995). In addition to growth responses, it is highly likely that species composition will change as a result of increasing CO_2 concentration (e.g., Bazzaz *et al*., 1989; Wong and Osmond, 1991).

Results obtained with different species and experimental conditions have shown that plant responses to increasing CO_2 concentration are likely to differ greatly among the ecosystems of the world. An assessment of the role of increasing CO_2 concentration in the global context requires quantification of the various factors that may increase or decrease the response of plants to CO_2 concentration. Most of the feedback effects are still inadequately understood and poorly quantified. However, plant-growth responses to doubled CO_2 concentration do not generally exceed 30% enhancement, even without negative feedback effects. The realized growth enhancements in response to the gradually increasing CO_2 concentration, therefore, are likely to amount to only a small gradual impact on terrestrial ecosystems.

A.3.   Soil Processes and Properties

Changes in climate will affect a number of crucial soil processes that will affect the ability of the soil to support particular natural or agricultural communities. The extent of these effects could have far-reaching consequences for the future distribution of fauna and flora, greatly changing distribution patterns and possibly resulting in new combinations of soils and vegetation (Tinker and Ingram, 1994). Soil development is likely to lag behind climate and vegetation change, so that in the medium term of decades to centuries, vegetation classes will probably often occur on soil types on which they are not currently found. It is not clear what consequences this mismatch between vegetation and soils will have for ecosystem function in the longer term.

Soil is formed through the interaction of many variables, the most important being parent material, climate, organisms, relief, and time (Jenny, 1941, 1980; Bridges, 1970; White, 1987). The strength and interactions of these variables differ across the world, producing many different soil types, each forming the basis of different habitats and each with different productive potential. Natural soil-forming processes (pedogen-

esis) occur slowly, but changes in the physical environment can lead to fundamental changes in soil types. Pedogenesis and the weathering of inorganic soil components in response to climate change have received insufficient scientific attention in the past, although these are very important for the development of new soil types, for nutrient release, and for many of the physical characteristics of soils (Arnold *et al*., 1990; Brinkman and Sombroek, 1995).

The rates of change of soil processes and properties resulting from climate change are likely to be different for different soil types (Stewart *et al*., 1990). Scientific assessments of the impacts of climate change on soils have largely been directed at soil processes that will respond most rapidly (over periods of months or years) and are thought to have the greatest effect on ecosystem functioning. These are principally changes in the soil water regime and turnover of organic matter and the related mineralization or immobilization of nitrogen and other nutrients.

Temperature has only marginal effects on reaction rates of most inorganic reactions in the soil, such as ion exchange, adsorption, and desorption, and increasing temperature itself, therefore, is unlikely to be important for the dynamics of inorganic nutrients. A change in soil moisture content, however, could significantly affect rates of diffusion and thus the supply of mineral nutrients such as P and K to plants. This could well alter the species composition of plants in natural systems and may require adjustments to nutrient management and fertilizer use in agriculture.

A.3.1.   Carbon Dynamics

The global pool of soil organic matter is estimated to contain about 1500 Gt of carbon (C) (Melillo *et al*., 1990; Adams *et al*., 1990; Anderson, 1992; Eswaran *et al*., 1993). This compares with estimates of 600–700 Gt C in aboveground biomass of vegetation (Melillo *et al*., 1990; Sombroek, 1990; Anderson, 1992; Schimel *et al*., 1994), 800 Gt C in the atmosphere, and about 40,000 Gt C in the oceans (Watson *et al*., 1990; Schimel *et al*., 1994). Most carbon in soils is associated with organic matter, although carbonate-C can also be significant in calcareous soils, and charcoal may be an important constituent in ecosystems subject to frequent fires. The amount of organic matter in soils is influenced by soil type, land use, and climate affecting the release or sequestration of CO_2 (see Box A-2 and Chapters 23 and 24).

Changes in organic carbon contents of the soil are determined by the balance between carbon inputs and carbon losses by organic-matter decomposition (soil respiration) rates. All terrestrial carbon inputs originate from plant products reaching the soil either as root exudates, dead roots, leaf litter, dead branches, or trees or indirectly as feces or bodies of animals. The annual input of carbon is thereby given by the amount of annual NPP minus the fractions of carbon that are removed from the system (e.g., in agricultural produce), lost during fires, respired by herbivores, or stored in increasing wood vol-

Box A-2. Terms Defining Carbon Dynamics

The amount of carbon taken up in photosynthesis is defined as the gross primary production (GPP). Some of this carbon is returned to the atmosphere as CO_2 during plant metabolism (autotrophic respiration), giving a net gain of carbon—the net primary production (NPP). Death and shedding of plant parts adds organic carbon to the soil, where it is decomposed by soil animals, fungi, and bacteria (heterotrophic respiration). The difference between NPP and heterotrophic respiration is the net gain or loss of carbon by the ecosystem and is termed the net ecosystem production (NEP).

umes on the site.

The great bulk of organic matter reaching the soil is respired by soil organisms within a few years, with the exact time course depending on climatic conditions and litter quality. The remaining organic matter is transformed into different forms with different decomposability. Some of it is highly resistant to decomposition, so it remains in the soil for hundreds to thousands of years even if conditions change greatly. Other material is slightly more labile, and some changes can greatly enhance its decomposition rate, leading to a loss of this fraction over years to decades (see the modeling studies of van Veen and Paul, 1981; Parton *et al.*, 1987; Jenkinson, 1990).

Changes in climatic conditions and land use generally affect both NPP and the rate of organic-matter decomposition. Soil organic matter increases if NPP increases more than decomposition rate, and soil organic matter decreases if decomposition rate increases more than NPP. However, any such changes in soil organic-matter content are very difficult to verify by direct measurements because of the high inherent variability of soil organic-matter content and because likely changes constitute only a very small fractional change of the amounts that are already in the soil.

Comprehensive data for soil organic-matter content in different soils across the Earth have shown that it increases with increasing water availability, and, for a given water status, it increases with decreasing temperature (Post *et al.*, 1982, 1985; Buol *et al.*, 1990). Both NPP and organic-matter decomposition are likely to be enhanced by increasing temperature, as all microbiologically facilitated processes are strongly affected by moisture and temperature. Annual soil respiration rates are likely to increase because of the lengthened season for breakdown of plant material and because increasing temperature strongly stimulates organic-matter decomposition (e.g., Berg *et al.*, 1993; Lloyd and Taylor, 1994; Kirschbaum, 1995), especially in arctic regions subject to permafrost (Reynolds and Leadly, 1992). Organic-matter decomposition is likely to be stimulated more than NPP (Kirschbaum, 1995). Consequently, although global NPP is likely to increase with global warming, soil carbon storage is likely to decrease at the same time, and this

could add more CO_2 to the atmosphere (e.g., Schimel *et al.*, 1990; Jenkinson *et al.*, 1991; Thornley *et al.*, 1991; Kirschbaum, 1993, 1995). On the other hand, none of these studies deals with the interactive effect of temperature and moisture limitations on decomposition rates. Should warming generally lead to moisture becoming more limiting for decomposition, then the effect of warming may be less pronounced than is suggested by these studies, which implicitly assume that moisture limitations will remain the same.

Other lines of evidence suggest that the carbon-storage potential of the terrestrial biosphere may not diminish in the future. Terrestrial carbon storage appears to have increased since the last glacial maximum (e.g., Bird *et al.*, 1994), and models of the possible distribution of biomes under future climatic scenarios with their associated observed carbon storage generally suggest increased carbon-storage potential in the future (e.g., Prentice and Fung, 1990; Smith *et al.*, 1992; King and Neilson, 1992).

Experimental work on the effect of increasing CO_2 concentration on soil processes has yielded divergent results (reviewed by van Veen *et al.*, 1991), but modeling studies (e.g., Thornley *et al.*, 1991; Kohlmaier *et al.*, 1991; Rastetter *et al.*, 1991; Polglase and Wang, 1992; Gifford, 1992; Kirschbaum, 1993) have consistently led to the result that increasing CO_2 concentration, via increased NPP, would lead to increases in soil carbon storage.

An important feedback is the mineralization of nitrogen and phosphorus (see also Section A.3.2). If increases in NPP lead to enhanced immobilization of nitrogen and phosphorus in soil organic matter, then the higher NPP will subsequently be reduced and the increased carbon input into the soil will not be sustained (Comins and McMurtrie, 1993; Kirschbaum *et al.*, 1994). Soil organic matter will then increase only marginally. On the other hand, if increasing CO_2 concentration can stimulate biological nitrogen fixation and mycorrhizal phosphorus uptake, then large and sustained increases in carbon input and consequently soil organic-matter content are possible. Limited experimental evidence suggests that nitrogen fixation may be enhanced by increasing CO_2 concentration (e.g., Norby, 1987; Arnone and Gordon, 1990; Thomas *et al.*, 1991; Gifford, 1994), so increasing CO_2 concentration may not make nitrogen more limiting as long as nitrogen-fixing plants are present in the ecosystem.

Photosynthesis in C_3 plants is more responsive to CO_2 concentration in warm than in cool conditions. At the same time, equilibrium amounts of soil organic matter change more with temperature at lower than higher temperatures (Jenny, 1980; Post *et al.*, 1982, 1985; Kirschbaum, 1995), so the net balance of effects may lead to soil organic-matter pools increasing in warm regions of the world and decreasing in cool regions (Kirschbaum, 1993).

Land use is significant in determining the balance between soils as a source and as a sink for carbon dioxide. Typically, about half the carbon is lost from soils after conversion of undisturbed for-

est or grassland to annually plowed cropland (e.g., Schlesinger, 1977, 1986; Buringh, 1984; Allen, 1985)—although this figure varies significantly with region, soil type, and kind of land-use change (e.g., Detwiler, 1986), and there may be greater carbon retention under minimum-tillage practices. A change in land use in the opposite direction can lead to sequestration of carbon in soils (see Chapters 23 and 24), although sequestration of carbon tends to be slower than carbon loss (e.g., King and Neilson, 1992; Smith and Shugart, 1993; Chapter 9, *Terrestrial Biotic Responses to Environmental Change and Feedbacks to Climate*, of the IPCC Working Group I volume). Conversion of forest or grassland soils high in organic matter to arable agriculture will inevitably cause a decline in soil organic-matter content and cause additional CO_2 to be released to the atmosphere. The associated mineralization of nutrients may allow increased plant growth, but large release of inorganic ions, especially if it is not synchronized with crop uptake, can add to the current problem of nitrate leaching into aquifers.

Soils are an important source of methane, contributing more than half the total emissions of 535 ± 75 Mt CH_4 yr^{-1} (Prather *et al*., 1994; see also Chapter 23). Soil methane comes from four main sources: (1) natural wetland soils (55–150 Mt yr^{-1}); (2) microbial degradation of organic substrates in paddy rice soils (20–100 Mt yr^{-1}); (3) landfills (20–70 Mt yr^{-1}); and (4) termites (10–50 Mt yr^{-1}). Soils also provide sinks for methane of 30 ± 15 Mt CH_4 yr^{-1} (Prather *et al*., 1994). The capacity of soils to oxidize CH_4 interacts in a complex manner with pH, land use, and the soil nitrogen cycle (Hütsch *et al*., 1994; King and Schnell, 1994). Future temperature increases in polar regions might lead to the release of methane currently contained in gas hydrates in permafrost regions both on the surface and in submerged regions (Collett *et al*., 1990; Kvenvolden, 1993).

The balance between the microbial processes of methanogenesis and methane consumption (Knowles, 1993) controls whether soils and paddy systems are a source or sink for methane. These biologically mediated processes are influenced by variables such as organic substrate supply, temperature, hydrologic conditions, pH, redox potential, aeration, and salinity—all of which are affected by climate change. Increasing temperature can alter methane fluxes by changing the rate of methane formation in lakes and wetlands and by altering the ratio of methane synthesis to methane oxidation. In addition, increased NPP provides more substrate for methane production, either from decaying plant matter or root exudations, and will provide more conduits for methane escape from lake and wetland sediments through the emergent plants, especially rice (Schütz *et al*., 1991).

A.3.2.   *Soil Nitrogen Dynamics*

Nitrogen can be added to the soil as inorganic fertilizer and organic manures and by wet and dry deposition from the atmosphere, or it can also be transferred from the atmosphere by biological nitrogen fixation (e.g., Bradbury and Powlson, 1994). Nitrogen is also released (mineralized) by the microbial decomposition of soil organic matter. Mineral nitrogen may be taken up by plants or re-absorbed by soil microorganisms; it may be leached as nitrate to ground and surface waters or emitted to the atmosphere in gaseous forms after nitrification, denitrification, or volatilization of NH_3 (Bradbury and Powlson, 1994). These processes are strongly influenced by temperature, soil moisture, plant characteristics, and, indirectly, by atmospheric CO_2 concentrations.

Nitrous oxide (N_2O) is formed in soils by denitrification and nitrification. Natural soils emit about 6 Mt N yr^{-1} and cultivated soils 3.5 Mt N yr^{-1}; together they probably contribute more than half of the total N_2O emitted to the atmosphere (Prather *et al*., 1994; Chapter 23). Much of the recent increase of atmospheric concentration of N_2O is attributed to increased use of legumes and N-fertilizers (Chapter 23). Soils also emit 12 Mt N yr^{-1} as NO_x, which constitutes about 25% of total NO_x emissions (Prather *et al*., 1994). Numerous environmental variables and agricultural practices influence the biological processes responsible for N-emissions from soils (Armstrong Brown *et al*., 1995). Environmental variables include soil temperature, moisture content, and aeration status, and agricultural management practices include fertilizer regime, cultivation method, and cropping systems (Chapter 23). Mineralization/immobilization requires moist soil, and denitrification requires water-saturated (anaerobic) soil or, at least, saturated microsites. Denitrification rates consequently increase with increasing soil water content. Soils are also likely to be a small sink for N_2O, although the size of this sink has not yet been satisfactorily quantified.

Nutrient-limited ecosystems, including most natural systems and many subsistence or low-input farming systems, are to some extent buffered against effects of global change: If climatic and atmospheric conditions become more favorable for plant growth, nutrient shortage will impose more serious limitations, whereas if climatic conditions change adversely, nutrients will become less limiting (Shaver *et al*., 1992). Consequently, NPP and total carbon storage of nutrient-limited systems is likely to be less affected by climate change than that of systems that are not nutrient limited.

Rastetter *et al*. (1992) have argued that NEP can only be positive if the total amount of nutrients in the ecosystem increases, if nutrient distribution changes from components with low ratios of carbon to nutrients to those with higher ratios, or if the carbon-to-nutrient ratio changes within vegetation or the soil.

The total amount of nutrients in an ecosystem may change as a result of altered rates of either inputs or losses. Nutrient losses may be prevented by immobilization in soil organic matter (although this also makes them temporarily unavailable for plants). Nitrogen gains may result from more favorable growth conditions that stimulate biological nitrogen fixation. Other nutrients may be gained through enhanced weathering of soil minerals. Nutrient availability may be increased through more extensive root growth and enhanced activity of mycorrhizal associations.

Levels of nitrogen and sulfur deposition are also increasing in many regions of the world through inputs from industrial pollution and other human activities such as agriculture. This may be having beneficial effects on NPP of many ecosystems, especially chronically nitrogen-deficient forests in high northern latitudes. While low rates of nitrogen input may have beneficial effects, ongoing inputs may reverse the initial gains through development of nutrient imbalances and further acidification of the soil (e.g., Ulrich, 1991, 1994; Linder and Flower-Ellis, 1992; Heath *et al.*, 1993).

A shift of nitrogen from vegetation to the soil has frequently been observed in CO_2-enrichment studies (e.g., Norby *et al.*, 1992; Diaz *et al.*, 1993). This is consistent with the theoretical notion that transiently increased productivity could lead to greater nutrient immobilization in soil organic matter and thereby shift the nutrient capital from the vegetation to the soil (Comins and McMurtrie, 1993; Kirschbaum *et al.*, 1994). Conversely, warming of soils with large organic-matter content may enhance decomposition rates and lead to the mineralization of nutrients (van Cleve *et al.*, 1981, 1990; Melillo *et al.*, 1993). This may stimulate plant growth and redistribute nutrients from soils to plants.

Carbon-to-nutrient ratios within soils are generally fairly stable, although they may differ between different ecosystems. Post *et al.* (1985), for example, document C:N mass ratios ranging from 9 to 30 in a comprehensive analysis of different global systems.

Although climate change may lead to small changes in the nutrient capital of soils or the ratio of carbon to nutrients, large changes are unlikely in the short term. Significant short-term changes in carbon storage are only possible where nutrient distribution changes between the soil and high C:N components, such as wood. Hence, in most systems, nutrient limitations will cause total carbon storage and associated NPP to remain similar to what they are currently. Only in the longer term (centuries) is the nutrient capital of soils likely to change so that climate again provides the essential determinant for NPP and total ecosystem carbon storage.

A.3.3.   Soil Biodiversity

Climate change could change the abundance of species within the soil microbial and faunal populations, although the direct effects from changes in soil moisture or temperature will be much smaller than those caused by changes in land use. It is not possible to predict whether there would be a change in biodiversity. However, in mid-northern latitudes (especially Europe), high inputs of industrial nitrogen are associated with major losses of mycorrhizal fungi (e.g., Arnolds and Jansen, 1992). These losses may make forests more vulnerable to drought and disease, which could be further exacerbated by climate change. The increasing concentration of atmospheric CO_2 could also change the composition of organic carbon compounds entering the soil from roots and root exudates, in addition to increasing its quantity. This may alter the species composition of the rhizosphere population—which, in turn, could alter the extent to which plant roots are infected by soil-borne pathogens. Whether such changes would be beneficial or harmful, however, is not known.

The question of whether microflora will change in line with the conditions or lag well behind them has not yet been fully addressed. Previous comparisons of microbial communities across different biomes have been largely confined to fungi and show that species composition is clearly related to biome type, even for the same biome in different continents (Kjoller and Struwe, 1982). Soil organisms with more specific characteristics—such as plant pathogens, symbiotic organisms—and soil fauna, may well be slower in adjusting to new conditions and may generally have slower migration speeds than higher plants. For plant pathogens and symbiotic organisms, there is the additional complication that they are dependent, to varying degrees, upon specific types of vegetation. A vegetation zone shift caused by temperature/precipitation changes will only have reached full equilibrium when both the vegetation and the appropriate microorganisms have established themselves together.

A.4.   Ecological Processes

Organisms interact not only with their physical environment but also with other organisms. The complicated sequence of dependencies and interactions among organisms has led to the description of ecology as the study of the "web of life." Impacts on a component of this web may be absorbed by a small part of the web, or they may lead to a cascade of effects throughout the web. This uncertainty makes predictions about the effect of climate change on complex ecological systems very difficult. In the following sections, we discuss some of the processes and interactions that most affect the response of ecological communities to climate change.

A.4.1.   Niche

All organisms have preferred places in which to live. These places, called the species' habitat, can be depicted on a map. A species' living requirements can be defined in a more abstract way based on aspects of the environment that define its habitat. These aspects may include a certain range of temperature, precipitation, soil conditions, and so forth. Each of these variables can be thought of as describing an axis in a multidimensional space, and the area or volume that describes the preferred habitat of a species is its niche (e.g., Austin *et al.*, 1990, Begon *et al.*, 1990). A species' "fundamental niche" encompasses all the environmental conditions in which it could potentially grow and reproduce if it were subject to no competition or other effects from other species (e.g., herbivory, disease). The fundamental niche is a consequence of an organism's basic physiological tolerances and ecological traits. In most ecosystems, where organisms compete and interact with

others, a species occupies a smaller space, called its "realized niche" (Hutchinson, 1957).

Climate change may cause the distribution of suitable habitats on a map to change. If temperature, moisture, or other climate variables at a particular location change, individuals at that location may find themselves now to be outside their fundamental niche. If a particular location falls outside the fundamental niche of a species, it is certain that individuals of this species will not be able to continue to reproduce and persist at this site. In other cases, the location may still fall within the fundamental niche but outside the realized niche. In this case, it is difficult to predict whether the species will be able to persist at this location because that will depend on which other species are able to persist or invade that site. In other cases, the location may still fall within the realized niche, and it is likely that the species will be able to continue to live at this site— although it may still be affected by changes in the distribution of other species. These assumptions are the basis of a number of models that attempt to predict the redistribution of organisms across the globe as a consequence of climate change (Box, 1981; Emanuel *et al.*, 1985; Prentice *et al.*, 1992, Cramer and Leemans, 1993).

A.4.2.   Interactions

A.4.2.1.   Competition

Individual organisms compete with each other for essential resources such as light, nutrients, and food, and for specific needs such as nesting space. Climate change may alter the competitive balance between species at a site by differentially affecting their effectiveness in the capture of resources or their efficiency in using them. Climate change may also result in the addition or loss of species from the site, thus changing the outcome of future competitive interactions. Higher CO_2 concentrations are predicted to favor C_3 species over C_4 species. Limited experimental results have shown that, although high CO_2 tends to favor C_3 over C_4 species, there is a wide range of responses and competitive outcomes even among C_3 species (Bazzaz, 1990). The fertilizing effect of widespread nitrogen deposition from industrial areas is a useful analogy for the impacts of climate change on the competitive interactions between species. In areas affected by heavy deposition, rapidly growing species of grasses and forbs are favored over slower growing, nitrogen-efficient shrubs (Chapin, 1980; Field *et al.*, 1992).

A.4.2.2.   Herbivory

Several aspects of herbivory might be affected by climate change. Some insect herbivores require cold periods during their life cycle, and these might be affected by warming. Higher rates of carbon fixation (see Section A.2.3) may provide more food for herbivores, but the quality of the food will be affected. It is likely that increased atmospheric CO_2 concentration will lead plants to produce tissue with a higher ratio of carbon to nitrogen (C:N) than under current conditions (Bazzaz, 1990; Field *et al.*, 1992). Many herbivores, especially insects, are limited by not being able to gather enough nitrogen in their diet (Scriber and Slansky, 1981), and a higher C:N ratio will force them to consume more carbon in order to gain a given amount of nitrogen. Some herbivores will increase the amount of tissue they consume to maintain their nitrogen uptake. In this case, damage by herbivores to their plant hosts is likely to increase. In other cases, herbivores will not be able to consume and digest enough plant tissue to maintain their required nitrogen intake. Their nutrition will suffer, and their population numbers will fall; they may even die out (Watt *et al.*, 1995). Some plants may also produce more defensive compounds, such as tannins and phenolics, when grown in elevated CO_2 (e.g., Lavola and Julkunen-Tiitto, 1994). Thus, in those cases, damage by herbivores will decrease in response to increased C:N ratios. Changes in the amount of herbivory will affect the nutrient cycle because nitrogen is cycled more rapidly but is also more likely to be lost to the atmosphere through volatilization when it passes through the guts of herbivores than through litter-decomposing organisms (Chapin and McNaughton, 1989).

Many insect herbivores have a boom–bust population cycle. They build up through several generations, with each generation larger, depleting their plant resources until the population is checked by lack of food, the onset of unsuitable weather (e.g., winter or drought), or natural enemies. If conditions after climate change allow the herbivore population to build up faster, much higher population levels and much greater damage may occur before they are checked. Conversely, some insect herbivores may be disadvantaged by climate change if, for example, the new conditions are more favorable to their enemies or the timing of growth or flowering of their food plants change. There is some evidence that stressful periods such as droughts that lead to reduced photosynthesis also lead to reduced production of compounds that normally help to control insect populations. Thus, some have predicted that under changed climatic conditions, stress periods will be more common and insect outbreaks more frequent (Mattson and Haack, 1987).

A.4.2.3.   Other Interactions

There are many other complex interactions within ecological systems. Parasites, disease organisms, and mutualists (i.e., organisms that mutually benefit each other, such as flowering species and their pollinating insects) are subject to the same constraints in relation to niche as other species. Climate change may advantage or disadvantage these species, with significant consequences for their host species. Schemes that help in the assessment of the likely effects of climate change on host–pest interactions are being developed (Landsberg and Stafford Smith, 1992).

A.4.3.   Communities and Their Dynamics

A.4.3.1.   Community

Any patch of land or ocean contains an assemblage of different

species that interact with each other in a variety of different ways. These assemblages are called communities. Just which species are part of a community depends on their niches—that is, whether they can tolerate the physical conditions of the patch and persist in interaction with the other species of the community.

There has long been a debate about the nature of communities and the degree to which they could be described as discrete entities. Communities were once compared with living organisms and described as tightly integrated assemblages of interacting species. Thus, a community was seen as an entity in its own right. If a community was perturbed by the loss or addition of some species, it would tend to recover to its previous composition or change to another discretely recognizable assemblage. The alternative view is that communities are essentially a collection of species, with each species behaving and interacting according to its own physiological and ecological potential. In this view, a community is a more fortuitous collection of species. Species continually invade or are lost from the community as populations fluctuate in response to weather, disturbances, and competitors.

These views about communities represent the end points of a continuum of ideas. Current thinking favors the view that communities are a collection of individual species, but an important ecological research theme is to identify rules that govern community structure (Drake, 1990; Keddy, 1992) and to seek groups of species that are ecological equivalents (sometimes called functional types; Smith *et al.*, 1993).

A.4.3.2. *Succession*

Communities are always changing, both as a result of a changing balance of interactions between the component species and in responses to disturbances. However, there are some patterns in the way communities respond to disturbances and change over time (i.e., succession). Succession was originally described as a sequence of organism-like communities, with one replacing another according to more-or-less strict rules (Clements, 1936). The endpoint of this succession of communities was called the climax community—determined, it was argued, by long-term climatic and soil conditions. Now succession is more often described as the outcome of a series of species losses and invasions as disturbances occur and conditions change (Whittaker, 1975). More emphasis is now placed on the stochastic nature of vegetation change, especially in ecosystems where disturbances such as fire or intense winds are common (Noble and Slatyer, 1980; Shugart, 1984).

The view of communities affects the methods used for predictions of ecological changes in response to global change. If communities change more like "organisms," it would be likely that under climate change one community will be replaced by another already known from elsewhere. This allows simple modeling by matching communities to environmental conditions and assuming that they will redistribute themselves with

climate change (see the discussion of Holdridge, etc., in Section A.4.4.2).

However, with a changed climate and disturbance regimes at a given location, conditions for some individuals will remain within their niche space, and they will continue to survive and reproduce at that location. Some species will be lost from the community relatively quickly as existing individuals die under the changed conditions (e.g., extreme temperatures, droughts, waterlogging) or disturbances (e.g., fires). Individuals of other species will be able to survive but not reproduce, and—although some individuals of long-lived species may persist at the site for decades or centuries—the species will eventually be lost from that location.

The loss of individuals from a community creates opportunities for others to invade. However, species best adapted to new conditions will not necessarily be among the early invaders because they may lack the dispersal ability to reach the site. The ability of species to invade new suitable locations varies greatly. Thus, it is unlikely that communities will move en masse. What is more likely is a sequence of invasions and losses leading to completely new communities, as was apparently the case over the past 10,000 years following the last Ice Age (e.g., Davis *et al.*, 1986; Webb and Bartlein, 1992).

A.4.3.3. *Migration and Dispersal*

As the climate changes, zones with suitable habitats for species will move in space. For example, as a result of warmer conditions, a species' niche space will be displaced away from the equator or further up mountains. An important issue in determining the nature of communities in the future is which species will be able to keep up with shifting climate zones.

Most plant species have poor dispersal ability, with the vast majority of seeds falling close to the parent plant. These species migrate very slowly—in most cases, far slower than anticipated shifts in climate zones—and they depend mainly on rare long-distance dispersal events to spread or invade new habitats. The rate at which many species spread after past disturbances, such as the ice ages, can be estimated by mapping the distribution of pollen left behind in bogs, lake sediments, and so forth (e.g., Davis *et al.*, 1986). Most species migration rates, estimated to be 10–30 km per century, are at least an order of magnitude less than the anticipated rates of shift in climate zones of 100 to 600 km over the next century (e.g., Solomon and Cramer, 1993). However, past migration rates are only a poor guide to the future because past rates may have been limited by the rate at which the climate changed. Also, the future potential for species migration is different than it was in the past. On the one hand, landscapes are now much more dissected by human activities than in the past, and this will hinder natural migration rates (di Castri and Hansen, 1992). On the other hand, human activities and technologies, such as motor vehicles and aircraft, provide sources of long-distance dispersal that were not present in the past.

Some species are already adapted to disperse widely and exploit any opportunity for invasion. They are often fast growing and quick to mature. These are often called tramp or ruderal species. They might be expected to do well during any reorganization of communities.

A.4.4. Ecosystems and Biomes

A.4.4.1. Ecosystems

A community and its abiotic environment is called an ecosystem. The abiotic and biotic components of an ecosystem interact, including significant effects of the biotic on the abiotic. For example, plant and animal communities often modify the soils. This process takes many decades or much longer but can eventually result in soils with properties that are closely matched with the communities they support. Where climate change causes significant spatial shifts of the range of species, these relationships may not be retained.

Ecosystem-level feedbacks may either dampen or amplify the growth response to individual climatic variables (Field *et al.*, 1992). The response of the ecosystem may depend on how the complex chain of interactions affects the cycling of nutrients and the efficient use of light and water. For example, if the availability of any one resource, such as carbon, increases, then other resources, such as nutrients, become relatively more limiting. Plants may respond to this by increased root growth, and this allocation shift may reduce the growth response of aboveground biomass to increasing CO_2 concentration.

Furthermore, if growth is determined more by the rate at which nutrients rather than carbon can be obtained, then even total plant production may not be increased. These constraints might eventually restrict the growth response of whole ecosystems to less than might be expected from short-term experiments on single plants or small communities (Körner, 1993). The overall functioning of the ecosystem may sometimes be insensitive to changes in particular species composition. One or more species may be replaced by others with more appropriate temperature optima or responses to CO_2, but the system as a whole may continue to function with broadly the same structure, physiognomy, and physiology.

Conversely, biological nitrogen fixation may be stimulated by more favorable growing conditions and lessen nutrient limitations. In systems that are not strongly nutrient limited, initial growth responses may allow greater leaf-area development, which allows greater light interception and further increases growth responses beyond that predicted from leaf-level responses.

More complex ecosystem responses may also occur. Initially increased growth may lead to reduced palatability of plant tissue for insect herbivores, which may either reduce or increase insect damage (see Section A.4.2.2) and thereby either act as positive or negative feedback on the initial response.

A.4.4.2. Biomes

Most observers readily recognize the similarity of ecosystems in the deserts of the world, no matter where they occur and how far apart they are. There are subtle differences between desert communities, such as the presence of cacti in some deserts and not in others and the diversity of reptiles between different deserts. However, all desert ecosystems operate within similar constraints, and their biota show similar adaptations to deal with these constraints. These similar ecosystems have been described with many different terms (e.g., biomes, life zones, biogeoclimatic zones) and emphases. Many studies relating to the global distribution of biomes and their redistribution under climate change define from 10 to 40 or more classes. Originally, their descriptions were based on the structure and appearance of the vegetation (Walter, 1962), but more recently climatic information has been used (e.g., Box, 1981; Cramer and Leemans, 1993).

A classification of biomes commonly used in global-change research was developed by Holdridge (1947). He used annual biotemperature (a measure related to the sum of temperatures above freezing throughout the year) and total precipitation to classify the vegetation of the world into 14 life zones or biomes. His scheme has been used as the basis for some predictions of the global-scale impacts of changed climates (e.g., Emanuel *et al.*, 1985), although more complex schemes have also been developed based on a wider range of climatic and soil parameters and a wider range of assumptions about the important variables delimiting the vegetation zones of the world (Box, 1981; Prentice *et al.*, 1992; Woodward, 1993; Neilson *et al.*, 1992).

As an example, Figure A-1 shows where some of the world's major biomes are found in relation to temperature and rainfall. In looking at the distribution of any biome in relation to climate, it must be recognized that annual mean values of temperature and precipitation provide only a rough guide to the requirements or tolerances of vegetation classes. In many instances, the distribution of classes also depends on seasonal factors, such as the length of a dry season or the lowest absolute minimum temperature, and on soil factors, such as water-holding capacity.

A.4.4.3. Ecosystem Breakdown

There has been progress in modeling the equilibrium distributions of biomes, which implicitly assumes that communities have time to sort themselves out. But the process of migration and reassembly may well lag behind the rate of climate change. Thus, climate-change studies based on the use of these equilibrium models can provide only a first indication of the direction or magnitude of expected changes.

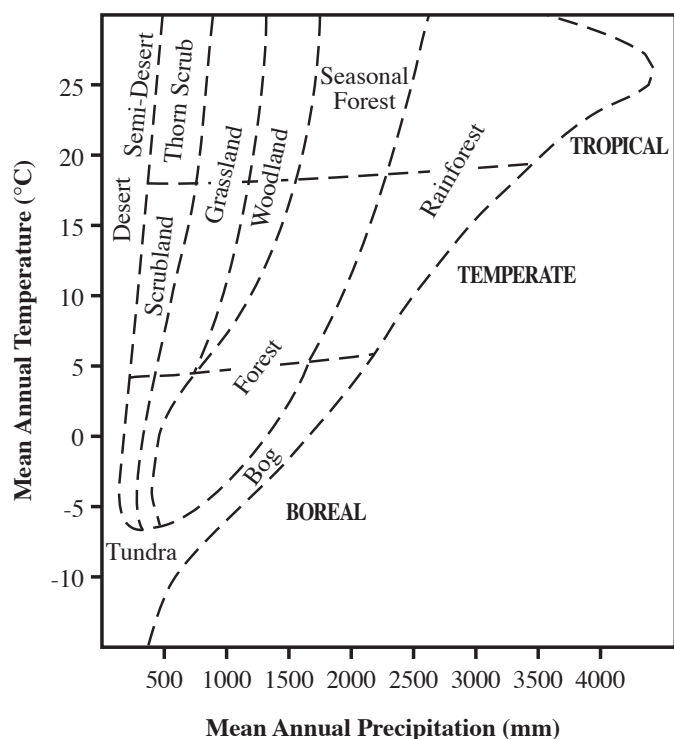In addition, there might be rapid breakdown of the existing

Figure A-1: This figure illustrates that mean annual temperature and mean annual precipitation can be correlated with the distribution of some of the world's major biomes. While the role of these annual means in affecting this distribution appears to be important, it should be noted that the distribution of biomes may also strongly depend on seasonal factors such as the length of the dry or the lowest absolute minimum temperature, on soil properties such as water-holding capacity, on land-use history such as agriculture or grazing, and on disturbance regime such as the frequency of fire (modified from Whittaker, 1975).

community structure via the loss of some species and invasion by others. The invading species will tend to be those best adapted to dispersing and invading, but not necessarily those best adapted to the most efficient use of resources in the prevailing conditions. This could lead to transient periods with less efficient use of light and water and less efficient recycling of nutrients. Temporarily lower biomass and transient release of carbon is likely to result from such a breakdown. Considerable scientific uncertainty remains about the length of these transients and the magnitude of the fluxes, but the fluxes could be significant (King and Neilson, 1992; Smith and Shugart, 1993).

A.5.   Conclusion

The preceding discussion offers a very brief overview of some of the main factors to be considered in relation to climate change. It describes the response of terrestrial ecosystems to the main aspects of climate change, and how these initial responses are affected by feedbacks from the soil and from interactions between different organisms. The importance of these factors varies greatly among different natural and socioe-conomic systems. This will be discussed in greater depth in the following chapters of this report.

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